Behaviour and mechanism of feeding of Lathonura rectirostris (Cladocera, Macrothricidae). V.N. Sergeev.(1971) Zool. Zh. 50, 1002-10

transl. by J.E.M. Horne.

We investigated behaviour in the feeding process and the functional morphology of Lathonura rectirostris O.F. Müller - one of the widely distributed species of macrothricids. L. rectirostris is a highly specialised species, adapted to life in thickets of aquatic plants. Feeding is possible by means of mechanical scraping-off or collection of particles and attached organisms with the help of the II pair of trunk limbs. Filtration feeding is absent. Movement along the substrate and attachment to a site are accomplished with the help of specialized supporting setae of the I and III pairs of limbs.

The adaptive significance of the structure of the limbs of Cladocera is impossible to appraise without a study of all the complex appendages in process of interaction. Primarily this appears especially in the external and anatomical structure, in connection with the functions of feeding, movement along the substrate in benthic forms, and respiration.

The current work is an attempt at morpho-functional analysis of the apparatus fof the trunk appendages of Lathonura rectirostris O.F. Müller. This highly specialized species, the method of feeding of which basically comes to the mechanical scraping-off and collection of epiphytic single-celled algae and particles deposited on the surface of aquatic plants. Specialization, as a result of which one must assume the decrease of competition on the part of invertebrates near in manner of life, is connected in L. rectirostris with changes in behaviour, structure and the operation of the complex of extremities, and also with changes in the structure of the carapace, the organs of movement in the mass of the water (II antennae) and the postabdomen.

The first descriptions and pictures of the trunk limbs of L. rectirostris were made relatively long ago (Fischer, 1848; Lilljeborg, 1853, 1900; Lund, 1871 Behning, 1912), but subsequently this species was never the subject of special investigation and is mentioned chiefly in faunistic lists.

Material for the current investigation was provided by animals collected in thickets of Elodea in a small production pond in Ropshe (a small village in the neighbourhood of Leningrad.)

Ecology and behaviour. L. rectirostris is an inhabitant of thickets of aquatic plants of small, often stagnant water bodies (Novikov, 1907; Filimonova, 1965; Vasil'eva, 1967; Brooks, 1966; Herr, 1917; Kuptsch, 1927; Lilljeborg, 1900; Lanchans, 1911; Scourfield & Harding, 1966). In large lakes, rivers, and reservoirs it inhabits analogous biotopes of the littoral shallow-water zone (Smirnov, 1965, 1966). In these conditions the importance of swimming is reduced, but the necessity arises for movement along the stem of the plant and for exact orientation in space. In the moment of collecting food L. rectirostris is in a position to control the situation in the surrounding environment: from behind, with the help of 'swimming setae' (fig.1.sn) in front, with the help of the setae on the branches of the II antennae (fig.1.sa) and from the side, with the help of the I antennae, which usually are directed to the side and nearly perpendicular to the longitudinal axis of the body. As regards the surface of the substrate any orientation is possible, in so far as in the process of feeding L. rectirostris is obliged (following the curvature of the stem) to take different positions, including also that when the animal is found head downwards.

The style of swimming of L. rectirostris recalls the movements of Latona or Sida: the powerful and relatively short antennae perform infrequent strong strokes "under themselves". L. rectirostris spends a great part of the time in crawling along the surface of the substrate; the II antennae are necessary for a quick change of place of attachment in case of danger. The musculature of the II antennae permits them to be withdrawn behind the head, where in the carapace there are special recesses, and to lower forward to the level of the abdominal margin of the carapace while the antennae are let down together and serve for cleaning the distal parts of the III and V pairs of limbs (fig.1,ssp: see also fig. 5, ssp, sp).

The form of the body of the animal is elliptical (fig.1). The cross section of the fore part of the body is of oval form, but more caudally the carapace forms lateral symmetrical bulges.

The bilateral compression of the shell, more noticeable by comparing the form of cross-section of L. rectirostris and other macrothricids (for example Ophryoxus gracilis G.O. Sars - see fig. 6, 1',2'), is an adaptation to existence in the mass of a thicket, when often the necessity arises to "squeeze through" a narrow chink. Chydorids, in which bilateral compression of the body is expressed to an even greater degree (Fryer, 1968), often inhabit an environment of filamentous algae, while L. rectirostris prefers the more "loose" thickets of Elodea, Sparganium, Menyanthes.

In the dorsal part the valves of the carapace form a narrow and sharp keel, stretching from the head (more precisely, from the place of attachment of the antennae muscles) along the spine to the posterior lower margin of the carapace (fig.1; see also fig.6,dc).

Of the two methods of movement: swimming and crawling, for L. rectirostris the latter is more important, inasmuch as movement along the substrate is necessary for feeding.

Movement along the substrate is possible with the help of the supporting setae (figs.1 & 2; see also figs 4 & 5; ssp - from the English 'supporting setae') of the I and III pairs of trunk limbs. The supporting structures of the I pair represent modified setae of the telopodites, i.e. the external parts (endites) of the endopodites of the limbs (fig.2, tl; 2',tl), having derived in benthic cladocerans a peculiar mobility and a comparative functional independence from the limbs altogether. The structure of the supporting setae is shown in fig.2,3'. Analogous setae of the III pair of limbs, utilized also for movement, belong to the armament of the endopodite, but differentiation on individual endites is expressed to a lesser degree (see figs. 4 & 5,ssp).

The technique of movement comes to the following: the I pair of limbs are raised upwards, deflected forwards and are lowered into contact with the substrate

- the animal obtains a point of support in front of itself, then as a result of contraction of the dorsoventral musculature the limbs of the body are drawn up in front. In the same way of movement the III pair of limbs also act, but not always synchronously with the I pair. The speed of movement at room temperature (20-21°) is from 0·14 to 0·65 mm/min. Young and smaller individuals travel always at a higher speed. The tempo of movement depends on the intensity of feeding and all things considered - on the quantity of food. During defaecation, which with abundant food takes place every 10-15 mins., L. rectirostris can stay without movement from 5 to 7 mins.

The co-ordination of movement of the limbs of the I pair and their position are controlled by the tactile setae of the exopodite (fig.1, ss 1, fig. 2, 2', ssl). The supporting structures of the I and III pairs of limbs (ssp) are utilized directly for pushing away from the surface, while the large claw-shaped setae of the V pair (see fig.5,sp), the postabdomen (p) and the epipodites of the V pair (ep 5) serve as additional support during movement. The postabdomen does not move out far beyond the bounds of the ventral and caudal margins of the valves, as is characteristic for O. gracilis and many chydorids. The movement of the postabdomen is limited and consists of travel in a vertical plane with small amplitude.

The centre of gravity of the body of L. rectirostris is situated comparatively low (especially in young animals), therefore the principal weight of the body is exerted on the supporting structure of the V pair and the postabdomen, while the crustacean obtains the possibility of greater freedom to manipulate by the supporting setae of the I and III pairs of limbs and the II pair. The structure of the supporting setae and the mobility of the limbs are used to fix firmly on to the stems and leaves of plants in any position, even abdominal side upwards, when the principal load is placed on the supporting setae of the I and III pairs of limbs.

In the case when L. rectirostris is moving along a stem the diameter of which is small by comparison with the dimensions of the animal, in the process of attaching and retaining in the necessary position the ventral margins of the carapace, covered with lanceolate setae (see fig.1) the length of which increases caudally, are drawn in. The setae, found on the middle part of the abdominal margin of the valve, during movement are deflected outwards.

In a cavity of the shell, on the abdominal side runs the ventral aperture, through which project the supporting setae of the I and III pairs of limbs, the tactile setae of the exopodites of the I pair and partially the epipodites of the IV and V pair. Together with the supporting structures of the I, III and V pairs of limbs and the postabdomen the armament of the ventral margin of the carapace contributes to the maintenance of a steady position during feeding and forward motion, not obstructing freedom of exchange of water, flowing around the epipodites of the IV, V and III pairs, that is especially important since positive respiratory currents are absent.

With the necessity to change place quickly L. rectirostris uses the II antennae. In the latter phase of the movement, i.e. the moment of attachment to a new place, the anterior part of the body, bearing the II antennae, over balances, and the crustacean is in contact with the substrate by the tactile setae of the exopodites of the I pair of limbs (fig.2,ss1) or the sensory setae of the II antennae (fig.1,sa).

The principal mass of food is collected by L. rectirostris from the surface of the stems and leaves of aquatic plants with the help of the II pair of limbs. Surveying the contents of 35 guts of females, collected on 23 August 1969, we discovered in them significant numbers of species of algae, principally epiphytic forms. Of the diatoms predominated: Achnanthes minutissima Kütz, Cymbella turgida (Greg.) ce., Gomphonema acuminatum Ehr., Achnanthes sp. Cocconeis disculus (Schum.) Cl., Tabellaria sp., Synedra sp., of the yellow-greens: Ophyocitium cochleare A.Br., Nephrodiella lunaris Pasch., Characiopsis malleolis Pasch. et Klug.; of the greens: Eremosphaera viridis De-Bary, Kirchneriella sp., of the blue-greens: Glococapse sp., Synechocystis aquatilis Sauv., Chlorogloea sp., Ch. microcystoides Geitl.

The quantity of cels in one gut is sometimes very great (more than 100 individuals of Achnanthes in the field of view of the microscope, magnification x 600). The content of the gut even in its anterior part often consists of fine particles, the identification of which is almost impossible. During prolonged maintenance in cultures it is possible to see, how the animal scrapes off the upper decomposed layer of the epidermis of the leaves and stems of the plants, the food value of which, evidently, consists in bacteria, dwelling in the mass and on the surface of the organic matter. We did not discover filamentous algae in the gut of L. rectirostris.

Structure of the trunk limbs and mechanism of feeding.

The trunk bears 5 pairs of differently constructed limbs (fig.1), of which the two latter pairs are frequently reduced and furnished with large epipodites, The I and II pairs generally lack epipodites. Only the II pair are utilized for collecting food and furnished with a form analogous in structure with filtering plates (fig.3sfs), the III and IV pairs take part in the sorting and elimination of unnecessary particles.

The I pair of trunk limbs appear part of the supporting-movement system. The armament of the epipodites of the limbs is separated into two unequal parts, one of which - the outer branch of the epipodite or telopodite (fig.2, 2' tl) serves only for attachment to the substrate and locomotion. The telopodite bears 4 unified supporting setae, 1 of which (the inner) is shorter than the rest. The plates, covering the distal parts of the supporting setae (fig.2,3') can shift in relation to one another, thanks to which the area of contact with the substratum is increased and the security of contact rises. The setae of the inner branch of the epipodites are arranged in like manner (fig.2, 1'), differing only in size: three of them situated on the inner margin of the limb and directed, differently from the remainder, upwards towards the food groove, are significantly shorter (fig.2,s.end.).

The internal branches of the epipodites function as a single organization - plates closing below the anterior part of the abdominal transporting path (the food groove). These parts of the limbs do not take part directly in the collection of food and the manipulation of it, but the position in orientation of three "shortened" setae (s.end) permits one to suppose that they serve for pushing forward particles situated in the food groove in front of the I limbs.

Numerous hairs and setae (fig.2,cl), covering the inner surfaces of the limbs, intercept particles diverted ventrally, preventing their loss. The exopodites are provided with long tactile setae (figs. 1 and 2, ssl). On the inner lateral surface of the limb is situated a seta (one on each limb), replacing possibly the maxillary appendage (si). The limbs are fastened to the body by narrow stalks, guaranteeing them a high mobility.

The II trunk limbs are the principal instrument for collecting and transporting food to the ventral surface of the trunk. The food groove is shortened and begins at the base of the III pair. The frequency of movement of the limbs and, consequently, the intensity of intake of food can be regulated within broad limits in relation to the degree of filling of the gut. At room temperature (20°) the limbs oscillate with a frequency of 92-144 strokes per minute.

An intricate complex of structures, working as a single system for the transfer of particles from the surface of the substrate to the food groove and along it into the region of action of the maxillules (fig.1,mx) and mandibles, comprises six groups of differently constructed and differently orientated series of setae (fig.3,3',tl,s,sg,s2,se2,sfs). The more distal part of the limb - the telopodite (tl) bears 3 long setae-scrapers of carinate form, used for making loose material and its transfer medially (fig.3,1'). With their participation are collected particles situated at the very edge of the valve, sometimes beyond its limits.

The movement of the limbs presents itself as a combination of synchronous movements in two planes; rotations around the vertical axis (fig.3,3',ab) and following after these raking under the trunk (fig.3, dotted arrows). In the first phase (the limbs are drawn together), the armature of the endopodites (fig.3,sg) moves parallel to the surface of the substrate scraping off algae adhering to it, particles, etc. The setae of series s2 and se2 transfer food, accumulated as a result of the cooperative action of the setae of the endopodites (sg) and telopodites (tl) of both limbs in the space between them, into the zone of action of the plates of the gnathobase (sfs). The setae of series s2 can, together with the filtering plates of the gnathobase, move in the region of the food groove (see fig.6,s2). In the subsequent phase (raking under the trunk) the terminal parts of the endopodites of both limbs (the gnathobases and their armature) are displaced from below upwards to the abdominal surface of the body and medially, and the plates of the gnathobase (sfs) are drawn together and move along the food groove forward, pushing through particles of food.

The III pair of trunk limbs (fig.4) differs sharply in structure from the first two pairs. The participation of the III pair in the collection and transportation of food is limited: the limbs are not utilized for catching or scraping off, but together with the IV pair they fulfil a no less important function in the sorting of the incoming material.

Determination of the food value of the mass, scraped off by the II pair, is made with the help of chemoreceptors (sensillae), positioned at the base of the gnathobases of the III pair (fig.4, sen). Sensillae have been described for many species of cladocerans (Fryer,1963; Smirnov,1967). The removal of unsuitable particles is a more complicated task, in the accomplishment of which the specialized setae of the gnathobase (fig.4,sg) of the III pair, the setae of the exopodites (fig.4,se) and the setae of the endopodites of the following (IV) pair take part.

The armament of th e exopodites of the III pair is adapted for arresting and discarding beyond the limits of the valves of the carapace particles of different sizes. The space at the base of the III pair is cleaned with the assistance of the setae of the gnathobases (fig.4,sg) and the setae of the more proximal endite (fig.4,spr), which move particles into the zone of action of the armament of the mobile exopodite (fig.4,e). The setae of the exopodite can be lowered to the level of the ventral margin of the carapace.

The supporting setae of the endopodites are analogous in structure with the corresponding structures of the I pair. On the outer lateral surface of the limbs are situated small epipodites (fig.4,ep).

The IV and V pairs of limbs are constructed most simply (fig.5). Their inner parts (endopodites) are frequently reduced. Both pairs are provided with huge epipodites of cylindrical form (fig.5,ep4,ep5). The epipodites of the V pair are usually pulled out beyond the limits of the carapace (see fig.1,ep5). The movements of the V pair are monotonous and consist of changes of the angle of slope of the limbs in relation to the substrate, dependent on the relief of its surface.

In contrast to Ophryoxus gracilis, in L.rectirostris the filtration process is absent. Characteristic of the simplification of all complex limbs, is primarily the partial reduction of the exopodites of III-V and the gnathobases of IV-V pairs of limbs, guaranteeing in O. gracilis the sealing of the filtering and suction chamber laterally and ventrally and the transportation of food forward (Sergeev, 1970).

The active extraction of food (in which the I and II pairs of limbs participate) is alike in both species and is adcomplished by the same agent, but the II pair of limbs of L. rectirostis are more mobile, since it has not the structure of a filtering complex.

FEEDING BEHAVIOUR AND MECHANISM OF LATHONURA RECTIROSTRIS (CLADOCERA, MACROTHRICIDAE)

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Summary

Lathonura rectirostris is a littoral weed-frequenting species of hydrophytes. Its feeding procees only at the expense of mechanical scraping and collecting particles by specialized «scraping» setae of endopodites of II pair of trunk limbs. Bacteria and unicellular algae (Diatomea, Xanthophyta, Chlorophyta and Cyanophyta) serve as a main food. Filtrational feeding is absent. The movement on the substrate is possible due to the joint activity of external parts of endopodites of I and III pairs of trunk limbs. The complex of trunk limbs is simplified as compared with that of typical filtrators.

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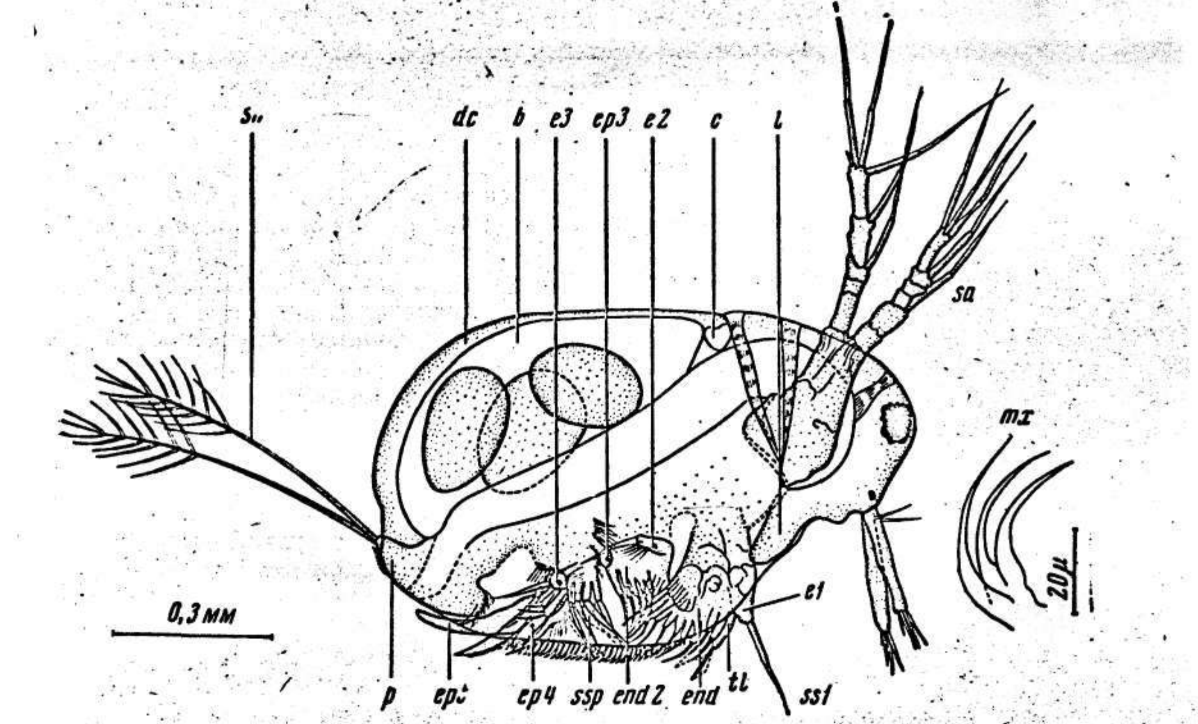

Fig. 1. STRUCTURE OF FEMALE

ssl - tactile seta, l - labrum, c - heart, e2 - exopodite of II limb, ep3 - epipodite of III limb, b - brood chamber, dc - dorsal keel, sn - sensitive (tactile) setae, p - postabdomen, ep5 - epipodite of V limb, ep4 - epipodite of IV limb, ssp - supporting setae, end 2 - endopodite of II limb, end - endopodite of I limb, tl - telopodite, el - exopodite of I limb, mx - maxillule, sa - sensory setae.

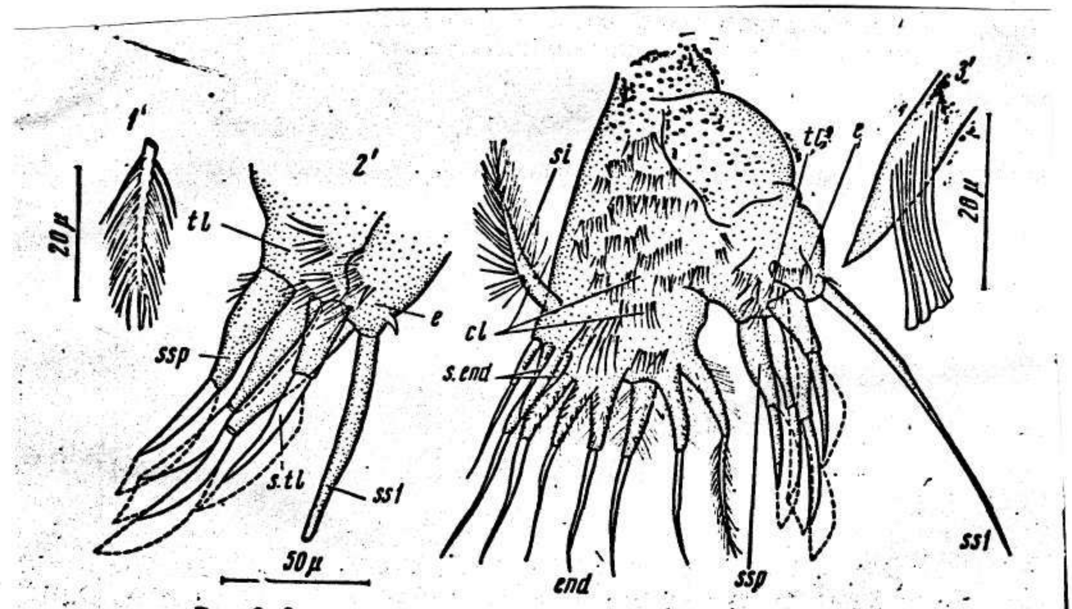

Рис. 2. I туловищная конечность самки (левая) изнутри

end — эндоподит, *ssp* — опорные щетинки, *ssl* — тактильная щетинка, *e* — экзоподит, *tl* — телоподит, *si* — максиллярная щетинка, *s. end* — медиальные щетинки, *cl* — щетинки на внутренней поверхности конечности, *s. tl* — щетинка телоподита; *1'* — структура щетинок эндоподита, *2'* — структура телоподита, *3'* — структура дистальной части опорной щетинки

Fig. 2. I TRUNK LIMB OF FEMALE (LEFT) FROM INSIDE

end - endopodite, ssp - supporting setae, ssl - tactile seta, e - exopodite, tl - telopodite, si - maxillary seta, s.end - medial setae, cl - setae on inner surface of limb, s.tl - seta of telopodite, 1' - structure of seta of endopodite, 2' - structure of telopodite, 3' - structure of distal part of supporting seta.

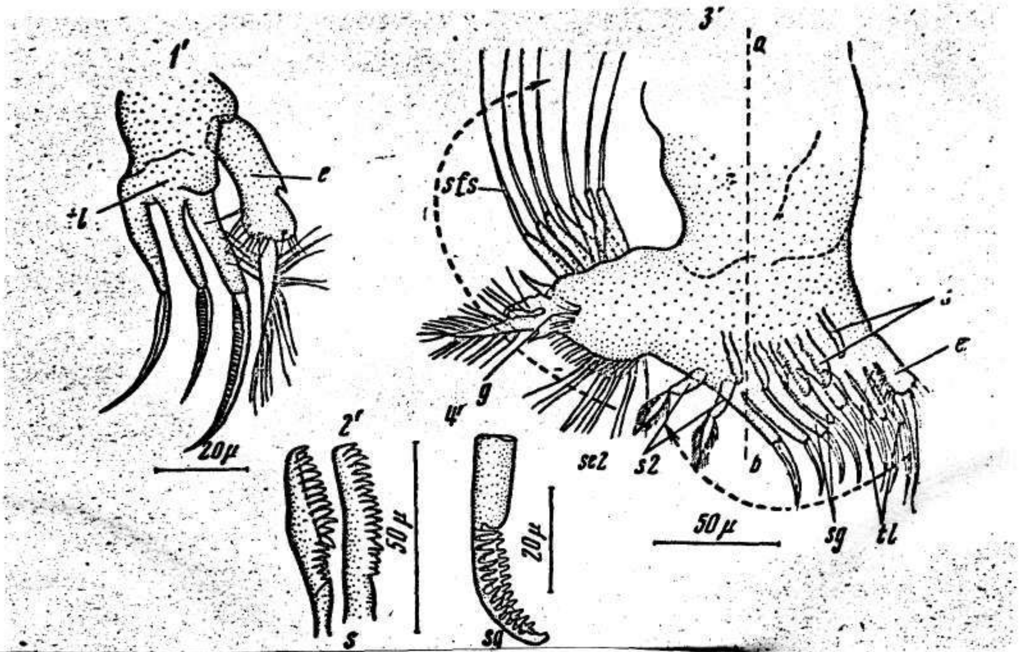

Fig. 3. II TRUNK LIMB OF FEMALE (LEFT) FROM INSIDE

s - medial seta, e - exopodite, tl - telopodite, s2 - transporting setae, sg - 'scraping' setae of endopodite, se2 - transporting setae of 2nd series, g - gnathobase, sfs - filtering plates of gnathobase; 1' - telopodite, 2' - structure of 'scraping' medial setae, 3' - general view of limb, 4 - structure of 'scraping' seta of endopodite; arrows show trajectory of movement of different parts of limb; dotted line ab shows the vertical axis, around which proceedds rotatio of the limb in first phase of movement.

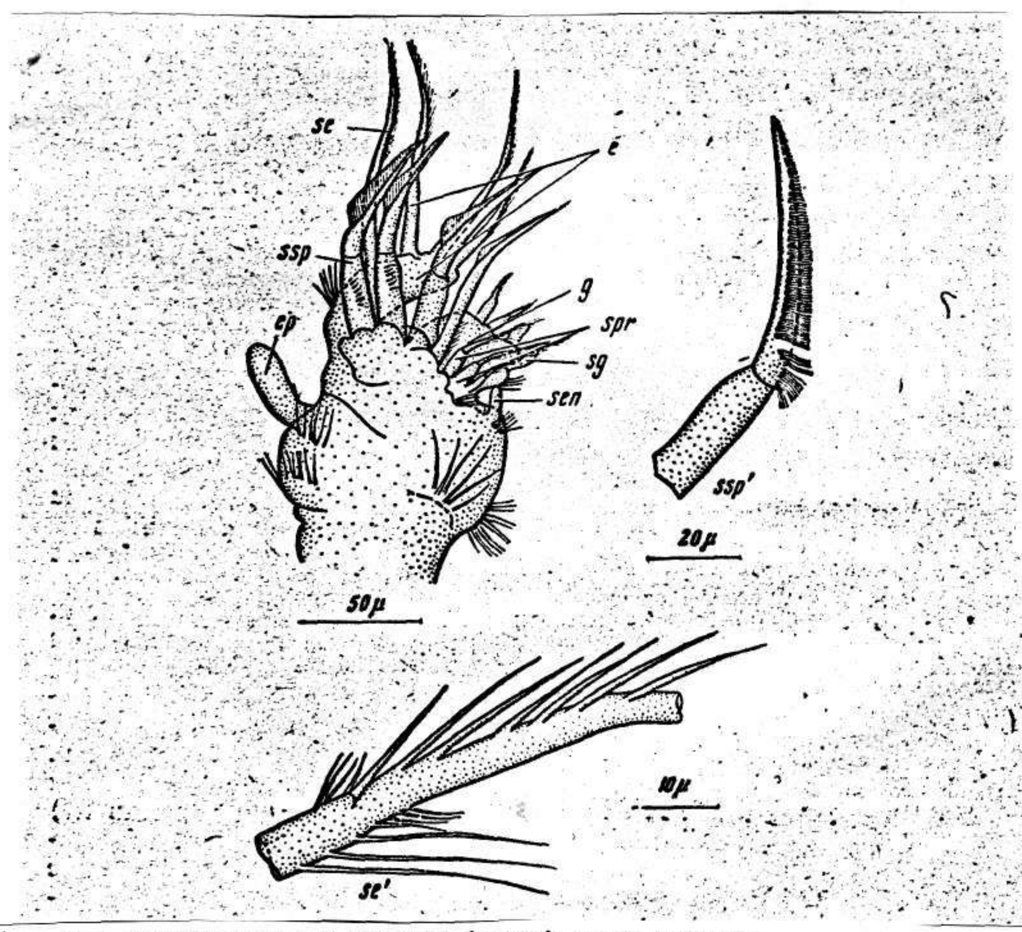

Fig. 4. III TRUNK LIMB OF FEMALE (LEFT) FROM INSIDE

sen - sensilla, sg - selecting setae of gnathobase, g - gnathobase, e - exopodite, se - seta of exopodite, ssp - supporting seta of endopodite, ep - epipodite, ssp' - structure of supporting seta, se' - structure of seta of exopodite, spr - selecting setae of endopodite, ssp - supporting seta of telopodite of III limb, sl - seta of exopodite of III limb.

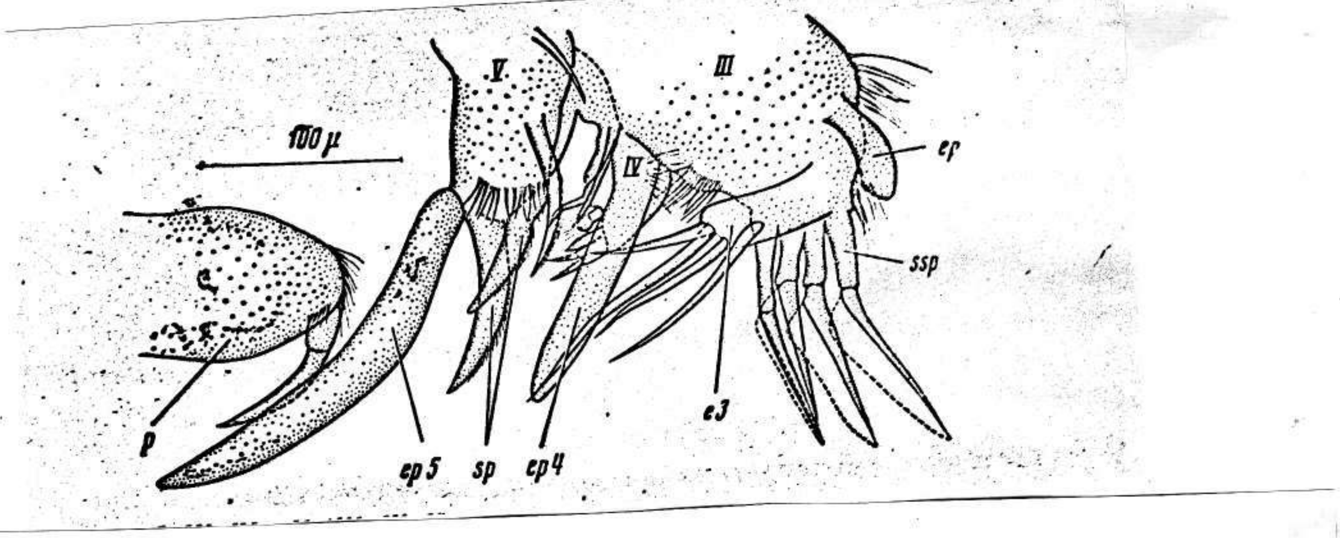

Fig. 5. III, IV AND V TRUNK LIMBS OF FEMALE (RIGHT) FROM OUTSIDE

p - postabdomen, ep5 - epipodite of V limb, sp - supporting structues of V limb, ep4 - epipodite of IV limb, e3 - exopodite of III limb, ssp - supporting setae of III limb, ep - epipodite.

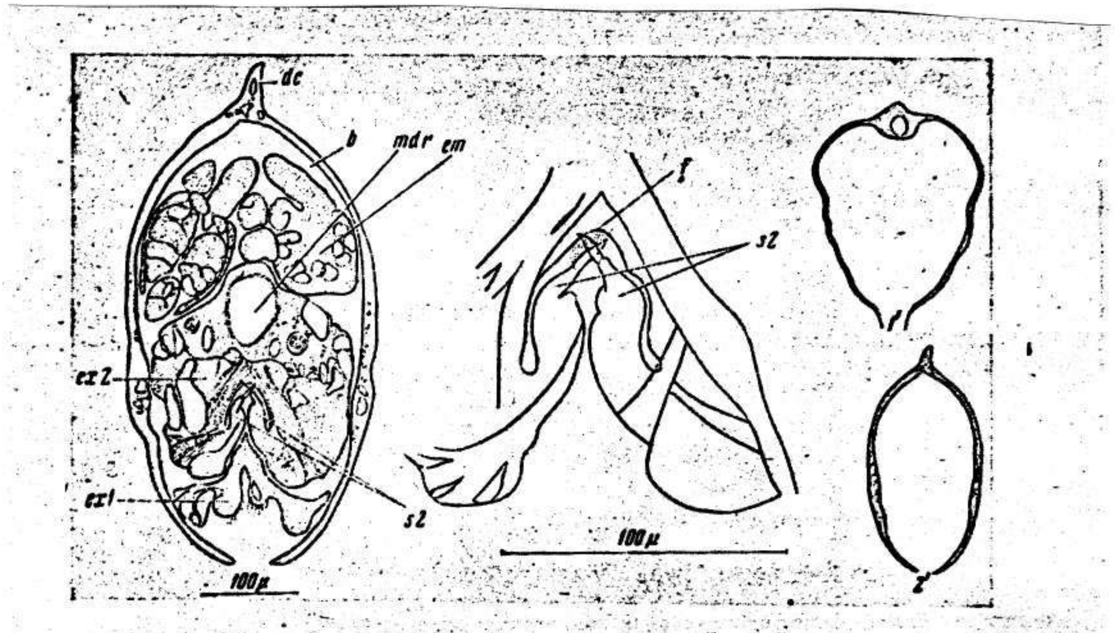

Fig. 6. TRANSVERSE SECTION IN REGION OF II PAIR OF LIMBS

s2 - transporting setae, em - embryo in brood chamber, mdr - midgut, b - cavity of brood chamber, dc - dorsal keel, ex2 - II limb, ex1 - I limb, f - food groove; 1' - transverse section of <u>Ophryoxus gracilis</u>, 2' - the same, <u>Lathonura rectirostris</u>

Notice

Please note that these translations were produced to assist the scientific staff of the FBA (Freshwater Biological Association) in their research. These translations were done by scientific staff with relevant language skills and not by professional translators.